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Mating behavior and three types of mating songs of the sandy beach-dwelling ground cricket *Dianemobius csikii* (Grylloidea, Trigonidiidae, Nemobiinae)

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Abstract

This study aimed to investigate the mating behavior of the sandy beach-dwelling ground cricket, *Dianemobius csikii* (Bolívar, 1901) (Orthoptera, Grylloidea, Trigonidiidae, Nemobiinae). The calling songs of males were recorded, and the temporal structures of the songs were analyzed. Subsequently, the courtship song and mating behavior of cricket pairs were observed. The calling song consisted only of monotonous chirps, while the courtship song consisted of similar chirps and ticks consisting of a single pulse. *Dianemobius csikii* exhibited a relatively longer courtship duration than other cricket species. The female stayed with the male for approximately 25 min while the male emitted the courtship song. The male then changed to the trill song, which is a continuous song, just before copulation. Copulation occurred within 10–40 s of the male emitting the trill song. The courtship behavior differs from that of other well-studied cricket species, such as Gryllinae. The findings of this study provide insight into the mating behaviors of crickets.

Keywords

calling song, courtship song, Orthoptera, sexual selection, Trigonidiidae

Introduction

In many animal species, males produce signals for mating (Andersson 1994). These males often produce different types of signals at different stages of reproduction (e.g., nuptial coloration and behavioral display in the guppy *Poecilia reticulata*, Houde 1997; some mating call types in frogs and toads, Kelley 2004). Understanding how and why multiple signals occur is currently a key topic in sexual selection research (Hebets and Papaj 2005, Bro-Jørgensen 2010, Partan 2013, Heinen-Kay et al. 2021). For example, different signals provide different information to receivers, including redundant backup information, distinct and complementary information, or signal amplification (Candolin 2003).

In crickets for several well-studied species, especially for Gryllinae, males produce three types of acoustic signals: calling, courtship, and aggressive songs (Alexander 1961, Gerhardt and Huber 2002). Calling songs are used for the long-range attraction of females and the demonstration of territory to other males, courtship songs are used in short-range courtship immediately prior to copulation, and aggressive songs are produced during fighting behavior with rival males (Alexander 1961, Gerhardt and Huber 2002). These song characteristics play a crucial role in the reproductive success of males.

The bulk of research on the acoustic communication of crickets has focused on Gryllinae, with few studies other cricket groups. However, several species of Trigonidiidae, which includes more than 700 species and inhabits diverse environments (Orthopterological Society of Japan 2006), have been reported to exhibit peculiar mating behavior and mating songs. For example, the swordtail cricket *Cranistus colliurides* Stål, 1861 (Orthoptera: Trigonidiidae) produces four distinct types of songs: calling, courtship, agonistic, and post-copulatory (Centeno and Zefa 2019, Centeno et al. 2021). Post-copulatory songs are rarely reported in crickets, and the function of the song is not known (Centeno et al. 2021). The striped ground cricket *Allonemobius socius* (Scudder, 1877) (Orthoptera: Trigonidiidae) exhibits courtship behavior depending on social environments: the males often omit the courtship song and copulate with females in solitary environments (Sadowski et al. 2002). Similarly, *A. socius* exhibits complex courtship behavior, including three types of courtship songs and two types of nuptial gifts (Mays 1971, Sadowski et al. 2002). Thus, the unique and diverse mating behaviors of Trigonidiidae make these species a valuable target for research on acoustic communication

The sandy beach-dwelling ground cricket *Dianemobius csikii* (Bolívar, 1901) is mainly distributed along the sandy beaches of Japan, Korea, and China (Orthopterological Society of Japan 2006, 2016). It is likely that the sandy beach environment has led to various adaptations in this species. For example, the body color of the cricket closely resembles the sand of its habitat (Fig. 1; Sato and Kuriwada 2022). Unfortunately, this species is feared to be extinct in some areas of Japan due to the disappearance of sandy beaches caused by coastal development (Fukuoka Prefecture 2014, Kyoto Prefecture 2015). Although mating behavior in

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other species of the same genus have been investigated (Kuriwada 2023), the ecology and behavior of *D. csikii* have not been widely studied; thus, the objective of this study was to describe the mating behavior of this cricket.

This study measured the temporal structures of the calling and courtship songs of *D. csikii* and examined the relationship between the structures of the courtship song and the copulation success of males. Furthermore, the male of *D. csikii* was observed emitting another type of song—a trill song—just before copulation that differed from their calling and courtship songs. The details of these results of the analyses of the songs along with observations of mating behavior of the cricket are reported here.

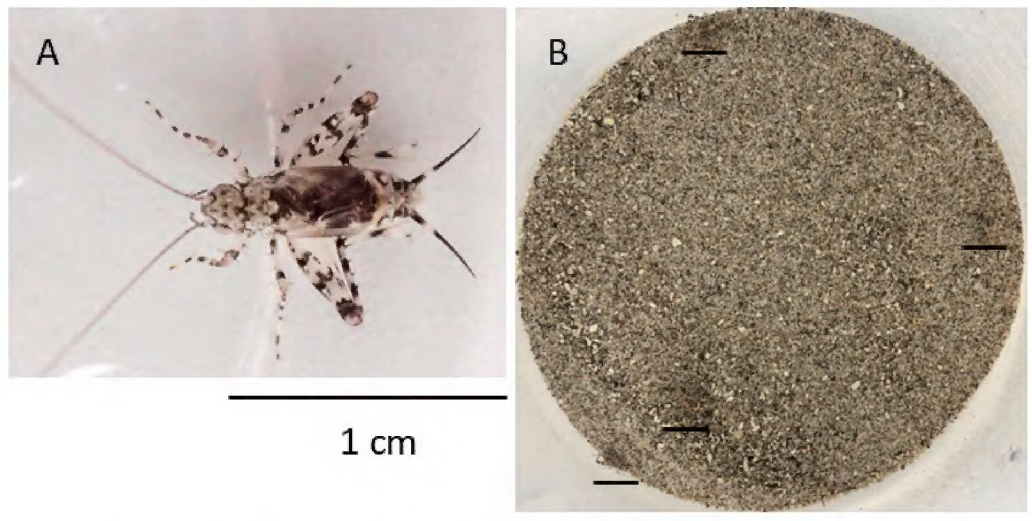

Fig. 1. A. Male *Dianemobius csikii*; **B.** Four *D. csikii* in the sand of their habitat; individuals indicated by black lines.

Materials and methods

Insect collection and rearing—Nymphs of *D. csikii* were collected from a sandy beach in Minamisatsuma city, Kagoshima Prefecture, Japan (31.4413°N, 130.2832°E), between late July and early August 2020. A total of 58 crickets were reared in a container (42 × 24 × 25 cm) at 27 ± 1°C under photoperiods of 15 h of light to 9 h of darkness (light cycle: 04:00 to 19:00). The crickets were given egg cartons for shelter, soil in a 200 mL plastic cup, guinea pig food (Marmot selection; Yeaster Co., Ltd., Hyogo, Japan), and cat food (Purina One Metabolic Energy Control; Purina, Kobe, Japan) provided *ad libitum*. Furthermore, the soil was sprinkled with water every 2–3 days to provide the crickets with a source of water and a site suitable for oviposition. The individuals used in this experiment were the third-generation progeny of the crickets originally collected from the beach. The final instar nymphs were reared individually in plastic containers (diameter = 6.0 cm; height = 3.0 cm), and the cups were checked daily for newly emerged adults. Adult crickets were kept in identical individual cups until the experiment began.

Recording of the calling song.—Using an uncompressed digital IC recorder with a 44.1 kHz sampling rate and a 16-bit dynamic range, the male calling song was recorded one to two days before the observation of mating behavior (RR-XS455; Panasonic, Osaka, Japan). The recordings were saved as WAV files. Each male container (6 cm diameter, 3 cm high) was placed with the IC recorder in a two-ply corrugated fiberboard box (inner side: 23 × 17 × 17 cm, outer side: 28 × 23 × 23 cm) that was physically, visually, and acoustically isolated from other cricket containers. All recordings were made at temperatures of 27 ± 1°C from 19:00 to 04:00, which corresponds to the dark period. Using Audacity v2.0.5 software (Dominic Mazzoni, Mountain View, CA, USA), seven components of the calling song were analyzed: time spent calling at night, chirp duration, chirp interval length, dominant frequency of the chirp, pulse duration, pulse interval length, and the number of pulses per chirp (Fig. 1A, D). Because pulse characteristics are important for species recognition in other cricket species (*Gryllus bimaculatus* De Geer, 1773, Schöneich et al. 2015), pulse characteristics were measured in addition to chirp characteristics. For analyses of chirp components, 10 measurements per component were randomly chosen. For analyses of pulse components, five measurements per component were randomly chosen. The mean of the chosen measurements was taken as the component value for the individual.

Observation of mating behavior.—Unmated males and females 8–14 d after their final molt were used for the observations. A focal male was placed in a plastic container (diameter = 12 cm, height = 19.0 cm), an unmated female was added to the container after 1 min, and the mating behavior of the pair was observed for 40 min. This process was repeated until 40 pairs had been observed . All experiments were started between 16:00 and 18:20 under fluorescent light. The timing fluctuated between 40 min and 3 h before the dark cycle, when crickets are usually active (Shimizu and Masaki 1997). Mating behavior was recorded using a video camera (SONY HDR-CX270V; Sony, Tokyo, Japan) held directly above the container at a distance of 50 cm. Latency to courtship was measured from the start of cohabitation to the production of a courtship song. During courtship, the male crickets switched from emitting the courtship song (Fig. 1B) to emitting the trill song, which has a different temporal structure (Fig. 1C). The trill song was defined as a song that was not interrupted by an interval from the time it was produced to the time of copulation. Courtship duration was defined as the time from the beginning of the courtship song to the start of the trill song. The courtship songs were recorded for 1 min using the same equipment described for the recording of the calling song. Latency to copulation was measured from the start of the trill song to copulation. Almost all of the males who copulated produced the trill song. I recorded the trill song in nine males. Copulation was defined as the contact of male genitalia with female genitalia during mounting behavior. Copulation was defined as successful when a spermatophore was attached to the female genitalia. If the pair did not initiate copulation after 40 min, it was recorded that the male had not copulated. The recorded courtship and trill songs were analyzed similarly to the calling song. The courtship song contained two types of song components (see Results section), and thus the number of repetitions of the same component type was recorded.

Statistical analyses.—To examine the effect of the temporal structure of courtship songs on copulation success, a generalized linear model with binomial error and logit link was implemented using R 4.1.2 (R Core Team 2021). The explanatory variables in this model were the components of the courtship song, and the response variable was copulation success (success = 1, failure = 0). The statistical significance of each coefficient was tested using the likelihood ratio test. Kendall's rank correlation was used to examine the correlation in each parameter between calling and courtship songs, and paired t-tests were used to compare the temporal structures of the calling and courtship songs.

Results

Temporal structure of the three song types.—The median time spent calling at night was 5.40 min (25–75% quantiles: 0–125.8 min,

N = 40). The calling song of *D. csikii* comprised only chirps (Fig. 2), whereas the courtship song consisted of a series of chirps interspersed with several short ticks (Fig. 3). The chirp consisted of approximately 65 pulses, while the tick consisted of one pulse. The pulse is the sound produced by a single rubbing of the forewings. The trill song maintained a continuous structure without interruption until copulation (Fig. 4). The pulse of the trill song was unclear (Fig. 4C) and could not be measured. The descriptive statistics for the three song types are listed in Table 1. The temporal structure of the courtship song did not affect copulation success (Table 2). There were no significant correlations between calling and courtship songs (chirp duration: $\tau = 0.25$, $p = 0.078$; interval length: $\tau = 0.13$, $p = 0.35$; dominant frequency: $\tau = 0.21$, $p = 0.15$; pulse duration: $\tau = 0.025$, $p = 0.87$; pulse interval: $\tau = -0.20$, $p = 0.20$; and No. pulse/chirp: $\tau = 0.016$, $p = 0.91$). The interval length of the courtship song was significantly shorter than that of the calling song (paired t-test: $t_{25} = 12.38$, $p < 0.001$), although the chirp duration of the courtship song was not significantly different from that of the calling song ($t_{25} = 0.47$, $p = 0.64$). The dominant frequency of the courtship song was significantly lower than that of the calling song ($t_{25} = 2.19$, $p = 0.038$). There were no significant differences in pulse duration or the number of pulses per chirp between calling and courtship songs (pulse duration: $t_{25} = 1.12$, $p = 0.27$; no. pulse/chirp: $t_{25} = 0.23$, $p = 0.82$). The pulse interval of the courtship song was significantly longer than that of the calling song ($t_{25} = 2.27$, $p = 0.032$). Based on the chirp and interval lengths, the chirp rate for the calling song was 1.09 chirps/s, and that for the courtship song was 1.43 chirps/s.

Mating behavior.—The mating behavior of the crickets began when a female approached a male. When the female body parts, including the antennae, touched the male, the male emitted a courtship song. The male continued to emit the courtship song for approximately 25 min without interruption, while the female remained nearby. Subsequently, the courtship song changed to the trill song. Approximately 10–40 sec after the change, the female mounted the male, and copulation occurred. Copulation lasted approximately 3 min. In 5 of 40 cases, the experiment was terminated 40 min after the courtship song began and before the cricket switched to the trill song. In these cases, no copulation was observed; however, the females remained near the males for the duration of the observation. Only one male successfully copulated without producing the trill song. Furthermore, 33 of the 34 males that emitted the trill song succeeded in copulation. In the one failed case, the female mounted the male, but the male spermatophore was not attached to the female genitalia, and the female ate the spermatophore. Figs 5, 6 present an overview of the mating process and the descriptive statistics of each mating behavior episode. No nuptial gifts, such as glandular exudate from males, were observed during mating behavior. No significant relationships were found between the parameters of the courtship song and copulation success (Table 2).

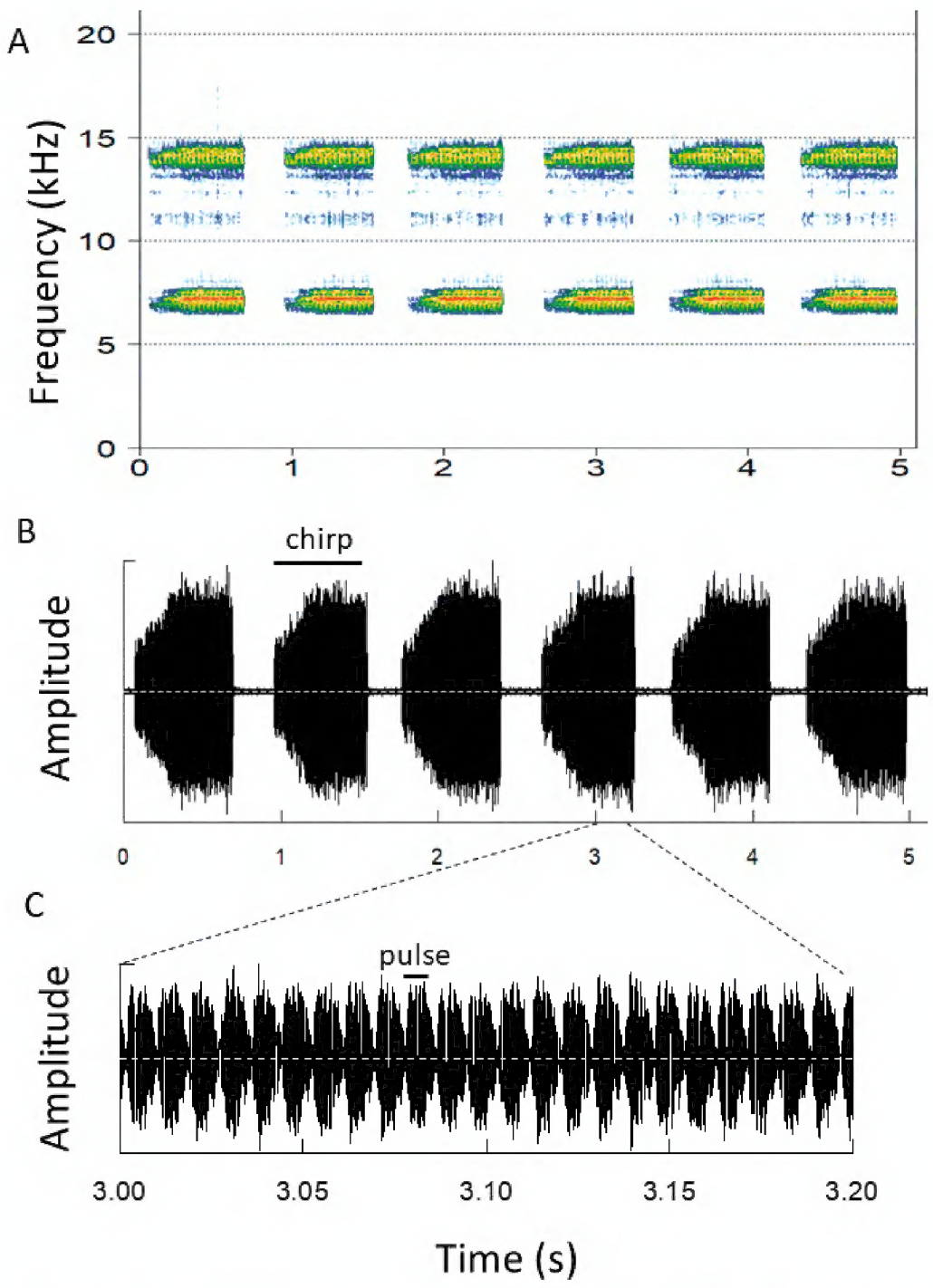

Fig. 2. Sound spectrogram (**A**) and oscillograms (**B** and **C**) of calling song of *Dianemobius csikii*. The oscillogram in **C** is an expansion of the time axis in **B**. Calling song consists of a series of chirps; a chirp consists of multiple pulses. Dotted lines **B** to **C** show the approximate corresponding times.

Discussion

In orthopteran insects, males produce multiple songs (calling, courtship, and aggressive songs), each used as a different behavioral signal (Alexander 1961, Gerhardt and Huber 2002). These three types of songs are considered to be the most common acoustic

Table 1. Descriptive statistics of the temporal structure of each song.

	Mean	SD	CV	N
Calling song				
Chirp duration (s)	0.59	0.056	0.095	26
Interval length (s)	0.33	0.081	0.240	26
Dominant frequency (kHz)	6.99	0.260	0.037	26
Pulse duration (ms)	5.45	0.817	0.150	26
Pulse interval (ms)	3.51	0.904	0.258	26
No. pulse/chirp	65.04	13.07	0.201	26
Courtship song				
Chirp duration (s)	0.56	0.17	0.30	40
Interval length (s)	0.14	0.024	0.16	40
Dominant frequency (kHz)	6.87	0.32	0.046	40
No. chirps†	17.92	22.19	1.24	40
Pulse duration (ms)	6.01	0.162	0.027	40
Pulse interval (ms)	4.05	0.105	0.026	40
No. pulse/chirp	66.15	26.24	0.40	40
No. ticks‡	6.78	3.30	0.49	40
Tick duration (ms)	9.21	4.32	0.47	40
Tick interval (s)	0.19	0.11	0.58	40
Trill song				
Dominant frequency (kHz)	6.50	0.20	0.031	9

† Number of chirps between ticks; ‡ Number of ticks between chirps.

signals widely shared by cricket species, including ground crickets (Taniyama et al. 2018, Hershberger 2021). In this study, male *D. csikii* also used courtship songs to court females at short distances but later changed the temporal structure to produce a trill song just before copulation. This is not typical cricket mating behavior. However, atypical behavior has also been observed in other ground cricket species (e.g., Mays 1971, Sadowski et al. 2002, Centeno, and Zefa 2019, Centeno et al. 2021, Hershberger 2021). Despite such findings, past studies of the mating behavior of crickets have been disproportionately focused on *Teleogryllus* and *Gryllus* species. Therefore, further research on mating behavior in various Therefore, further research on various Orthoptera species could reveal diverse mating behaviors. Moreover, phylogenetic comparisons may reveal the evolutionary trajectories of mating songs.

The production of mating songs in crickets requires high energetic expenditure (Hoback and Wagner 1997). The song also attracts predators, parasitoids, and conspecific females (reviewed by Zuk and Kolluru 1998). Because of the high cost and risk, only males in good condition can produce distinctive mating songs and the correlation of male quality with the song characteristics ensures the signal honesty (Maynard-Smith and Harper 2003). In addition, males often produce different types of signals according to the mating contexts (Candolin 2003). Some adaptive significances have been proposed for the existence of multiple mating signals: the multiple signals may provide different information to receivers, including redundant backup information, distinct and complementary information, or signal amplification (Candolin 2003). For example, different signals provide information on different aspects of male quality (Wagner and Reiser 2000). In the present study, no significant correlations were found between the temporal structures of the calling and courtship songs. A possible explanation for this is that different signals provide information on different aspects of male quality rather than redundant information on the same aspect of male quality. The present study also found no significant relationship between the temporal structures of courtship songs and copulation success. These results suggest that female preference does not rely on certain structures in courtship songs because those structure may not reflect the true quality of the male because the song structure may not honestly reflect male quality. On the other hand, however, the observation is not choice test with playback experiment; hence the suggestion is limited. Because the present study only provided one male for a focal female, the female had to mate with him for fertilization. Further studies identifying correlations between song components and male traits and/or their effects on offspring are needed.

The likely function of the trill song identified in the present study is to induce female mounting for mating because almost all pairs copulated within 40 s after males switched to the trill song. In contrast, the function of the courtship song may be to allow the female to assess the quality of the male, as the male emits the courtship

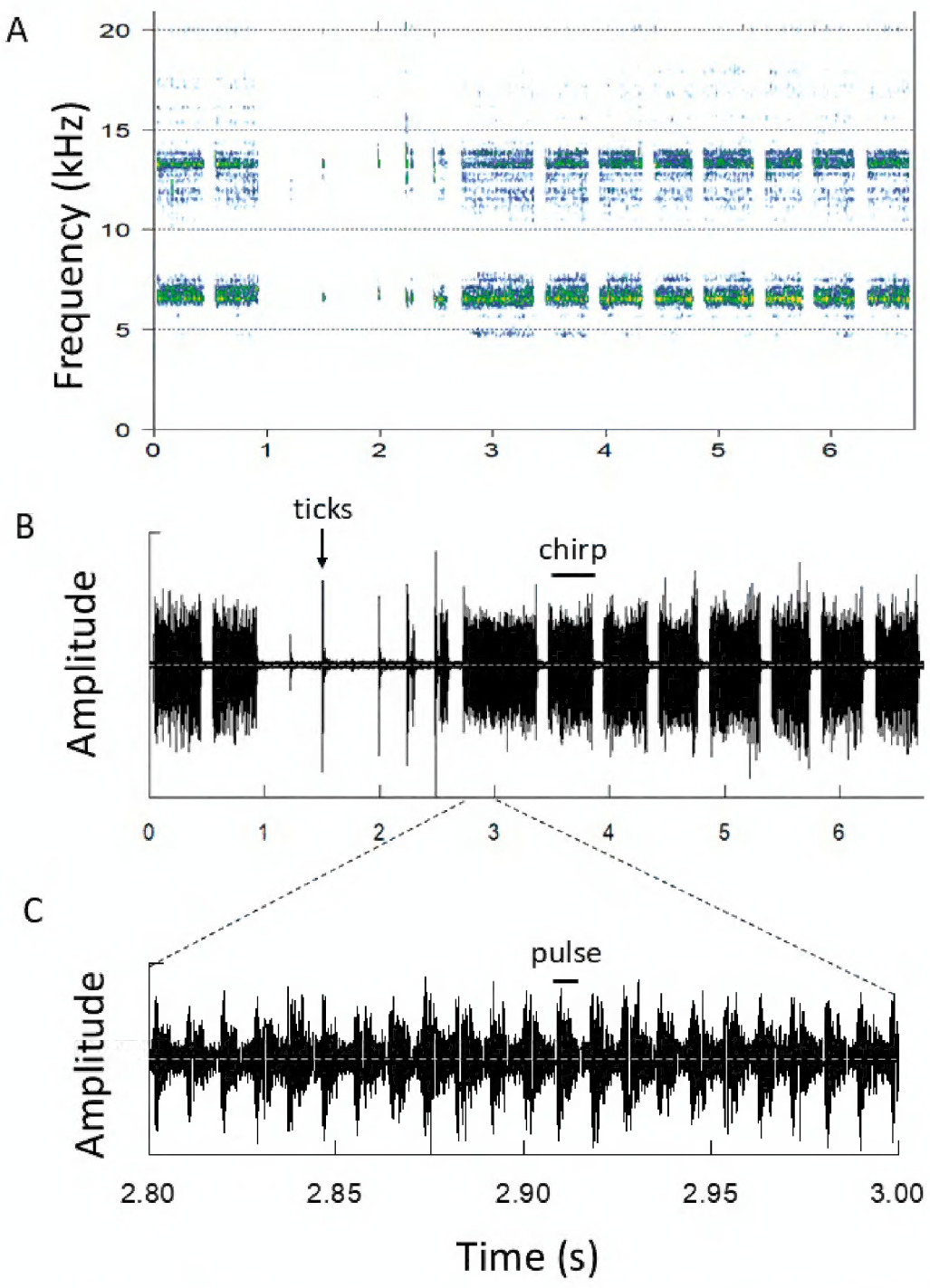

Fig. 3. Sound spectrogram (**A**) and oscillograms (**B** and **C**) of courtship song of *Dianemobius csikii*. The oscillogram in **C** is an expansion of the time axis in **B**. Courtship songs were sometimes interspersed with ticks between chirps (**B**). Dotted lines **B** to **C** show the approximate corresponding times.

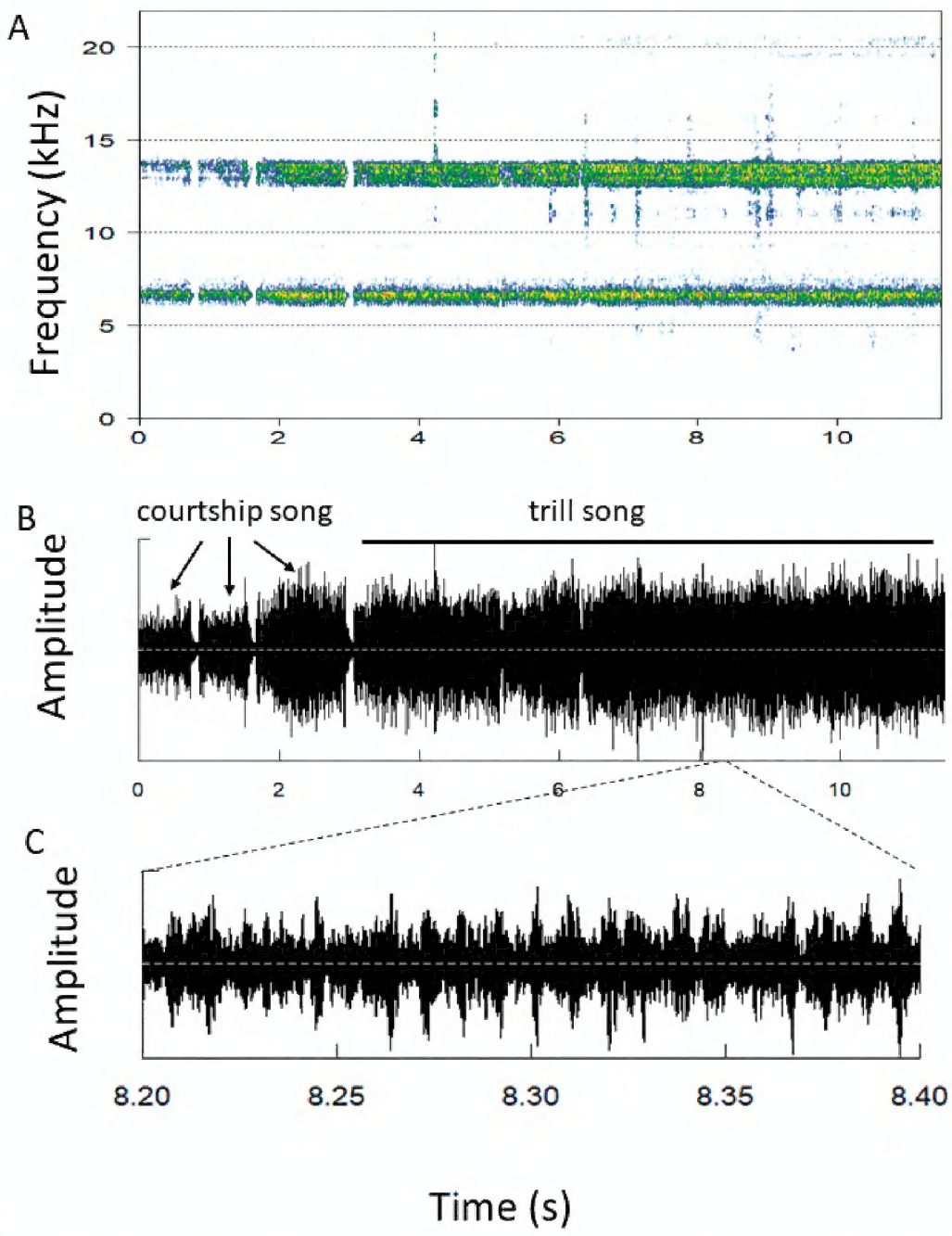

Fig. 4. Sound spectrogram (**A**) and oscillograms (**B** and **C**) of trill song of *Dianemobius csikii*. The oscillogram in **C** is an expansion of the time axis in **B**. Once the courtship song changed to the trill song, the trill song was continuously emitted until copulation began. Dotted lines **B** to **C** show the approximate corresponding times.

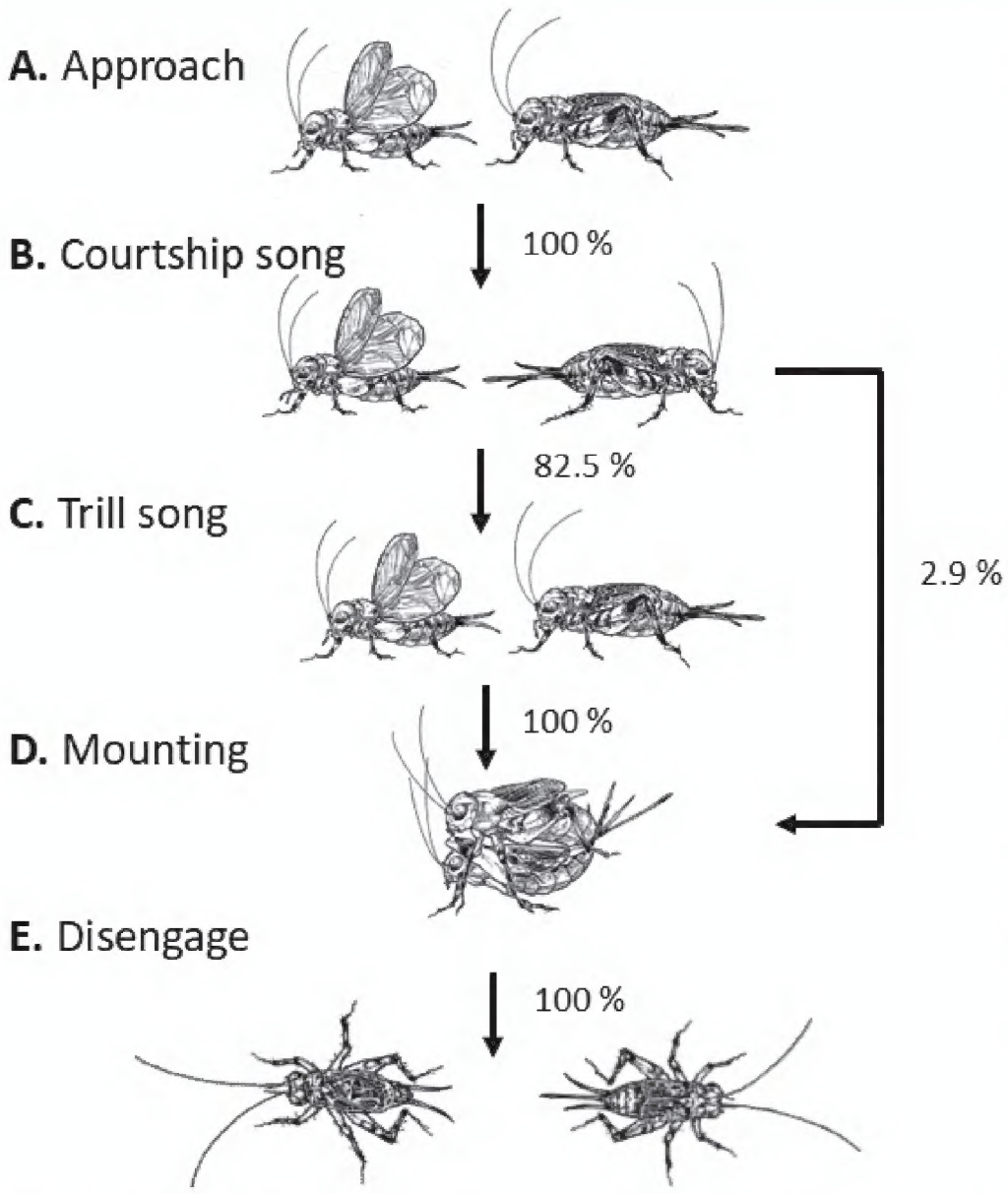

Fig. 5. Mating behavior of *Dianemobius csikii*. **A.** Male emitting the calling song. **B.** When a part of the female body touches that of the male, the male emits the courtship song. The female stays by the male during the courtship song. All males (40 individuals) emitted a courtship song when approached by a female. **C.** Approximately 25 min after the male begins to produce the courtship song, most males (34/40 = 85%) switched to the trill song. Only one male (1/34 = 2.9%) copulated without production of the trill song. **D.** The female mounts and copulates with the male approximately 20 s after the beginning of the trill song. All females (34 individuals) mounted the male when the male emitted the trill song (although only one male failed to pass the spermatophore). **E.** When copulation ended, the female dismounts and leaves the male. Illustrations by Yu Hirayama.

Table 2. Effect of the temporal structure of the courtship song on copulation success. Results were obtained using generalized linear model testing.

Explanatory variable	t-value	P-value
Chirp duration	0.41	0.68
Interval length	0.39	0.70
Dominant frequency	0.55	0.59
No. chirps†	1.04	0.31
No. ticks‡	0.47	0.64
Pulse duration	0.59	0.56
Pulse interval	1.42	0.17
No. pulse/chirp	1.22	0.23
Tick duration	0.61	0.55
Tick interval	0.12	0.91

† Number of chirps between ticks; ‡ Number of ticks between chirps.

song for approximately 25 min while the female stays nearby. Most of the pairs had a courtship song lasting approximately 25 min. However, some pairs (12.5%) did not change to the trill song after 40 min, and copulation did not occur. Identifying the factors that lead to the change in the song, such as micro-movements or female chemical cues, is an important area for future research.

Specific environments may cause the evolution of novel song types and mating behaviors. For example, owing to the abundance of acoustically orienting parasitoids, two new male morphs have been observed in the Hawaiian populations of the Pacific field cricket *Teleogryllus oceanicus* (Le Guillou, 1841) producing a novel purring song (Tinghitella et al. 2018, Fitzgerald et al. 2022). Similarly, the evolution of long courtship durations and the trill song in *D. csikii* may be related to habitat characteristics. Alternatively, such songs may evolve through phylogenetic constraints or Fisherian arbitrary processes of mate choice independent of environmental characteristics. Comparisons of mating behavior with other closely related species, such as *D. nigrofasciatus*, may be necessary, but such research is hindered by a lack of information on the courtship behavior of these species. Future research should also consider whether the mating behaviors reported here are advantageous in sandy beach environments such as the habitat of *D. csikii*.

Availability of data

The data used for this study are available from the corresponding author on request.

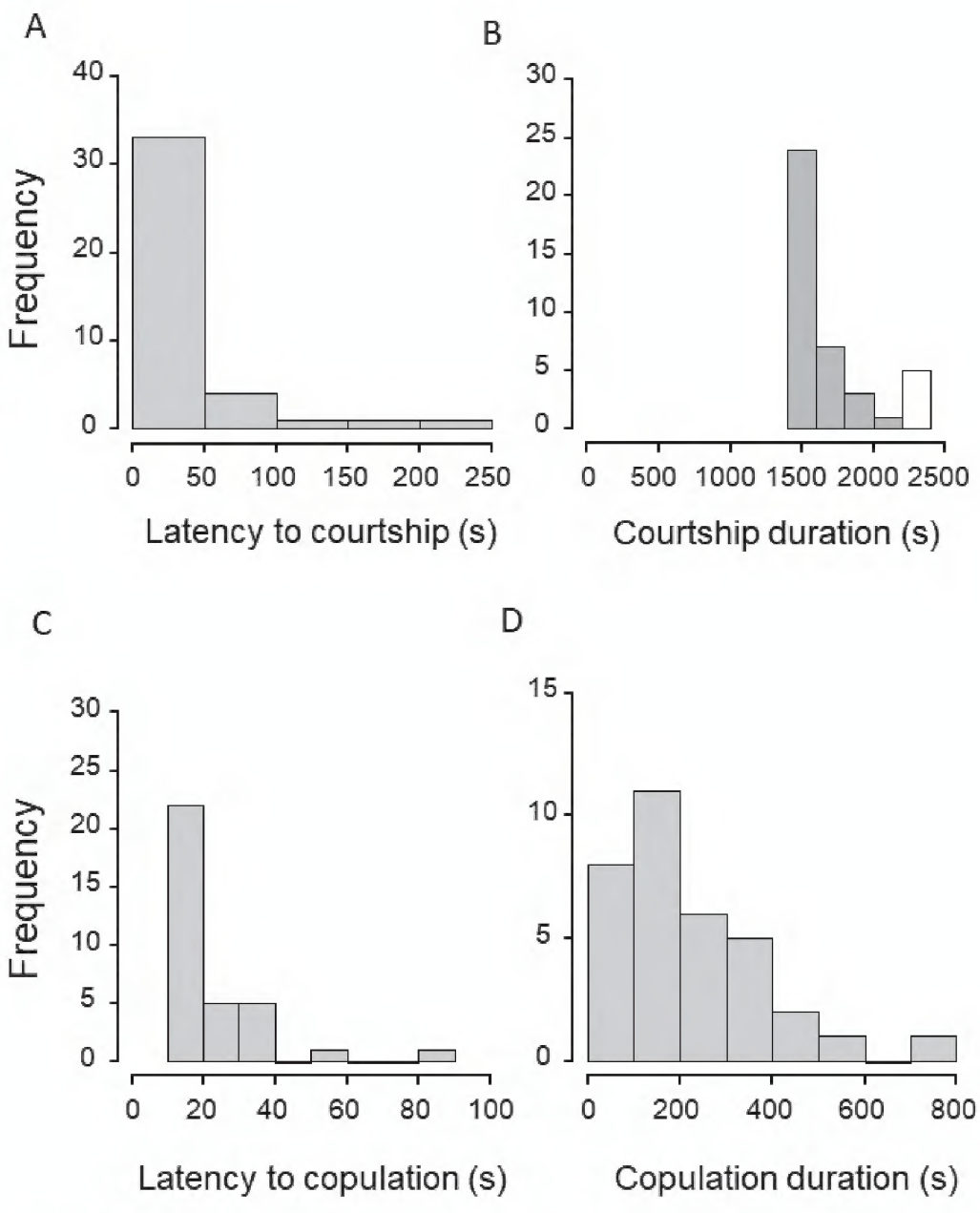

Fig. 6. Histogram of mating behavior parameters of *Dianemobius csikii*. **A.** Latency to courtship, **B.** courtship duration (i.e., time from start of courtship song to change to trill song), **C.** latency to copulation (i.e., time between trill song and copulation), and **D.** copulation duration. The white bar indicates no copulation within 40 min (**B**).

Ethics approval statement

All experimental procedures in this study were conducted in accordance with the guidelines for the use of animals in research in Kagoshima University.

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